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Brain growth patterns in the La Plata River dolphin (*Pontoporia blainvillei*)

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Abstract

There have been relatively few studies of brain growth in cetaceans despite the potential importance of these studies for understanding cetacean brain-behavior relationships and mammalian brain evolution in general. Among terrestrial mammals, and within the Primate Order most notably, high encephalization levels and long juvenile periods of dependency are associated with a prolonged period of brain development. In the present study, brain growth patterns in the La Plata River dolphin *Pontoporia blainvillei*, were examined. Results show that *P. blainvillei* possesses a more mature brain throughout development than that previously reported for other odontocete species. Furthermore, the pattern of brain development in *P. blainvillei* fits into the general pattern of association between adult EQ level and brain maturation in both cetaceans and primates.

Introduction

Brain size is one of the most important variables in mammalian life-history evolution. Yet there have been relatively few studies of brain growth in cetaceans despite the potential importance of these studies for understanding cetacean brain-behavior relationships and mammalian brain evolution in general. Several authors have noted that, among mammals, brain size is highly positively correlated with a number of life history variables, including body size, duration of gestation period, weaning age, length of juvenile period, and life span (see Harvey *et al.*, 1986 for an extensive review of this literature). In addition, brain size is positively correlated with several behavioral ecological factors such as social group size (Dunbar, 1993; Sawaguchi & Kudo, 1990) and complexity of dietary strategy (Clutton-Brock & Harvey, 1980; Eisenberg & Wilson, 1978, 1981; Gibson, 1986; Mann *et al.*, 1988).

Among odontocete species, adult levels of encephalization (a measure of relative brain size accounting for brain-body allometry) are correlated with such behavioral ecological factors as social group size (specifically, pod size) in a similar way to that which is found in primates (Marino, 1996). Yet, the relations among brain size, body size, and the life history variable of gestation length among odontocetes are not similar to those found in terrestrial mammals (Marino, 1997). Therefore, some studies suggest that cetaceans may be characterized by both similar and dissimilar life history and behavioral ecological patterns from other mammals, but strong tests of how cetaceans contrast with other mammals await substantially more information on how brain size and morphology is related to behavior in cetaceans.

One of the areas in which there is relatively little known regarding cetaceans is that of brain growth patterns. Among terrestrial mammals, patterns of pre- and postnatal brain growth are correlated with adult encephalization levels and cognitive-behavioral dimensions, such as length of juvenile period, degree of behavioral plasticity, and, information processing complexity or intelligence. That is, among terrestrial mammals, and within the Primate Order most notably, high encephalization levels and long juvenile periods of dependency and learning are associated with a prolonged period of brain development (Harvey *et al.*, 1986; Joffe, 1997). The modern human brain, which is approximately seven times larger than expected on the basis of body size, requires approximately 18 years to grow from just under 25% of its adult weight at birth to its full weight (Spector, 1956). In contrast, the brain of a rhesus macaque monkey (*Macaca mulatta*) which is only about twice as large as expected for its body size, requires a relatively shorter period of time to grow from just under 60% of adult weight at birth to its full weight (Crile & Quiring, 1940; Hofman, 1983; Schultz, 1941). Regardless of its underlying basis, the pattern of relation between duration of brain growth and adult measures of intelligence is a robust one among terrestrial mammals. Therefore, because cetaceans represent a highly encephalized mammalian group (Marino, 1998; Worthy & Hickie, 1986), the question of whether cetaceans follow the typical mammalian pattern in terms of brain size growth and adult encephalization levels is important for testing the generality of existing hypotheses regarding the reasons for the relational pattern between brain growth and adult encephalization among terrestrial mammals.

The few studies that have been done with cetaceans point to intriguing differences and similarities in brain growth patterns among odontocetes and between odontocetes and other mammals. Ridgway & Brownson (1984) reported that *Tursiops truncatus*, *Delphinus delphis*, and *Orcinus orca* possess neonatal brain weights of 42.5, 57.0, and 53.0% of adult brain weight, respectively. These findings preliminarily place the developmental pattern of the brain of *T. truncatus* between that of humans and most primates, but that of *D. delphis* and *O. orca* at approximately on a par with some monkey species, showing that there is considerable variation among odontocete species in terms of relative brain development. Furthermore, Pirlot & Kamiya (1975) found that the brain weight/body weight ratio of *Pontoporia blainvillei* is significantly lower than that of *Stenella coeruleoalba* at birth and throughout the lifespan. On the basis of these findings they postulated that the pattern of brain growth and its relation to adult brain size in odontocetes may reflect differences in the information-processing demands of a pelagic versus inland existence, or, more generally speaking, differences in various habitats.

In the present study, the brain growth pattern of the La Plata River dolphin or Franciscana (*Pontoporia blainvillei*) is examined. Brain and behavioral patterns of the Platanistidae, in general, are less well known than in some of the more extensively studied odontocete species. Although some studies have been done involving measures of adult brain size in *Pontoporia* (Kamiya & Yamasaki, 1974; Marino, 1998; Pilleri & Gihr, 1970), with the exception of Pirlot & Kamiya (1975) little is known about brain growth patterns in this species. Furthermore, because many aspects of the lifestyle of Platanistids contrast with other odontocetes, particularly more pelagic species, the study of brain-behavior relations and brain growth patterns in a Platanistid species offers a potentially informative comparative analysis.

Methods

The data set for the present study consists of 36 *P. blainvillei* specimens from the National Museum of Natural History (NMNH) collection at the Smithsonian Institution. Normative data on age, body weight and body length for *P. blainvillei* was used to exclude ill, emaciated, or gravid specimens from the sample (Brownell, 1984; Harrison & Brownell, 1971; Kasuya & Brownell, 1979). Endocranial volume was measured for each specimen using a standard volumetric technique by which the cranium is filled with plastic beads (Radinsky, 1967). Endocranial volume has been used extensively as a measure of actual brain volume or weight (because the specific gravity of brain tissue is close to the value of one volumetric measures can yield reasonably accurate estimates of weight) (Dart, 1923; Gingerich, in press; Jerison, 1973, 1978; Marino, 1997, 1998; Passingham, 1975; Radinsky, 1967; Uhen, 1996). Reliability of cranial volume was determined by taking two cranial volume measurements of 20 specimens separated by 1–3 days. The mean difference between the first and second measure was 1.28%. Therefore, the reliability of the present sample of endocranial volume measurements was well within the 2% error typically reported in the literature for primate endocranial volumes.

Endocranial volume overestimates actual brain volume because it includes non-neural structures, particularly the vascular rete mirabile. No data currently exist which offer an estimate of endocranial rete volume in Pontoporia or any of the other Platanistids. However, a preliminary analysis of average endocranial rete volume for 29 non-Platanistid odontocete specimens suggested that the rete accounts for approximately 10% of total endocranial volume. This result coincides with other findings (Uhen, 1996). Therefore, in the present analysis 10% was subtracted from the total endocranial volume of each specimen to yield an estimated brain weight (here on in referred to as brain weight) for each specimen that may more accurately reflect actual brain size. It must be borne in mind, however, that this is a rough estimate based upon the only data we can bring to bear on this estimate at present.

Body length and weight data for each specimen were obtained from the NMNH collection files. Because previous studies (Marino, 1998) have shown no significant difference between male and female odontocetes in relative brain size and related measures, the results of the present study represent combined data for the sexes. Brain weight was regressed on body length in order to assess the pattern of change in brain weight as a function of change in body growth or maturity. Although not an infallible measure of maturity, body length was used instead of body weight because body length is less subject to the fluctuations that affect body weight, e.g. seasonal blubber thickness.

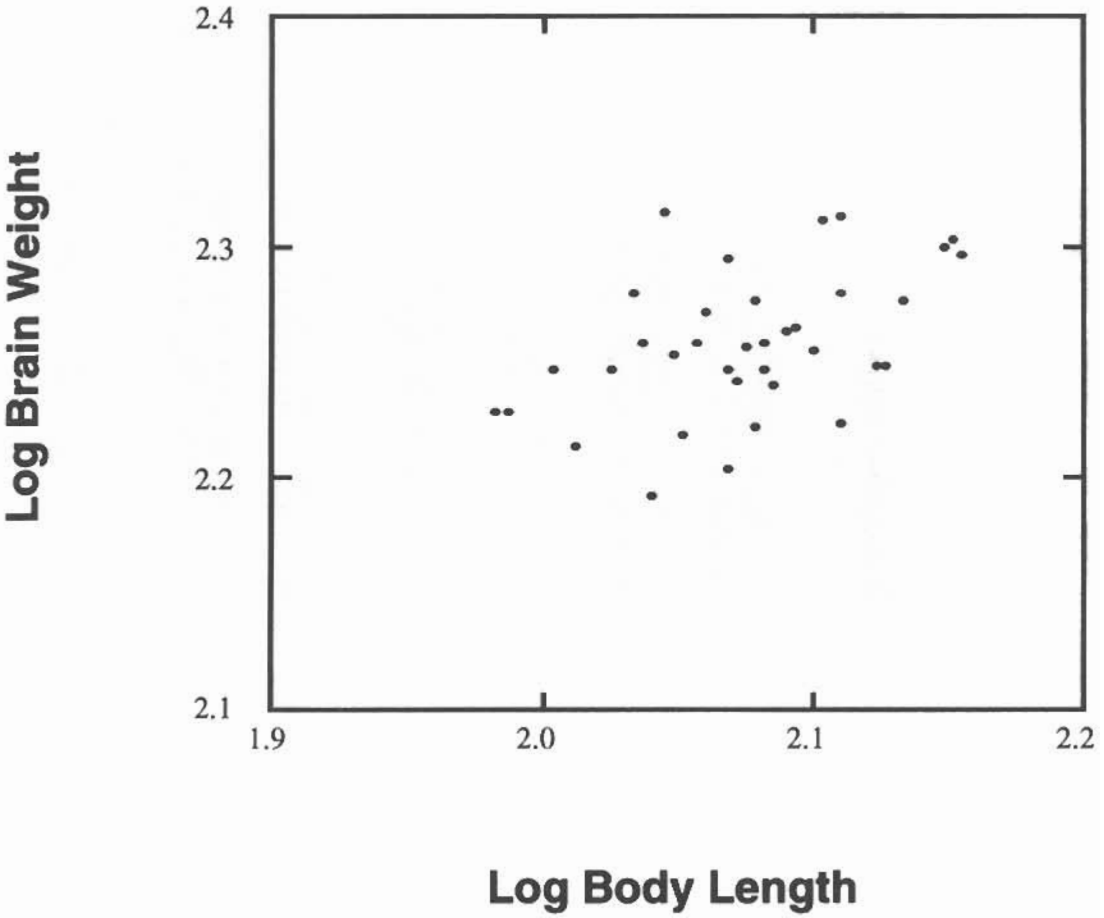

Figure 1. Log brain weight regressed on log body length for *P. blainvillei*.

In addition, in order to describe, in a general way, brain growth patterns in *P. blainvillei* within the context of life history stages, mean brain weight as a percentage of mean adult brain weight was analyzed within the context of specific age categories. Each specimen was classified according to the following age categories—neonatal (birth), weaning, sexual maturity, and physical maturity—on the basis of its body length and body weight. When there was a discrepancy between these two measures, body length was used for the same reasons described above. Specimens were classified directly into one of the four age categories if body length fell within a 5% range of the mean value for that age category. If a specimen's body length fell outside that range and midway between the mean values for two age categories, it was classified as an 'in-between' age, e.g., weaning-sexual maturity. If a specimen's body length fell outside that range and closer to the earlier age it was classified as a late substage of the earlier age, e.g., late weaning, and if closer to the later age it was classified as an early substage of the later age, e.g., early sexual maturity. However, when specimens were categorized according to the above procedure, there were only eight age categories (i.e., early weaning, weaning, late weaning, weaning–sexual maturity, early sexual maturity, sexual maturity, sexual maturity–physical maturity, and physical maturity) which the sample specimens represented and therefore of which the analysis was comprised.

Results

A least-squares regression of brain weight on body length yielded an allometric exponent or slope of 0.528, and a coefficient or y-intercept of 118.55, with a Pearson correlation coefficient of 0.481. Figure 1 depicts the relationship between log brain weight and log body length for the present sample.

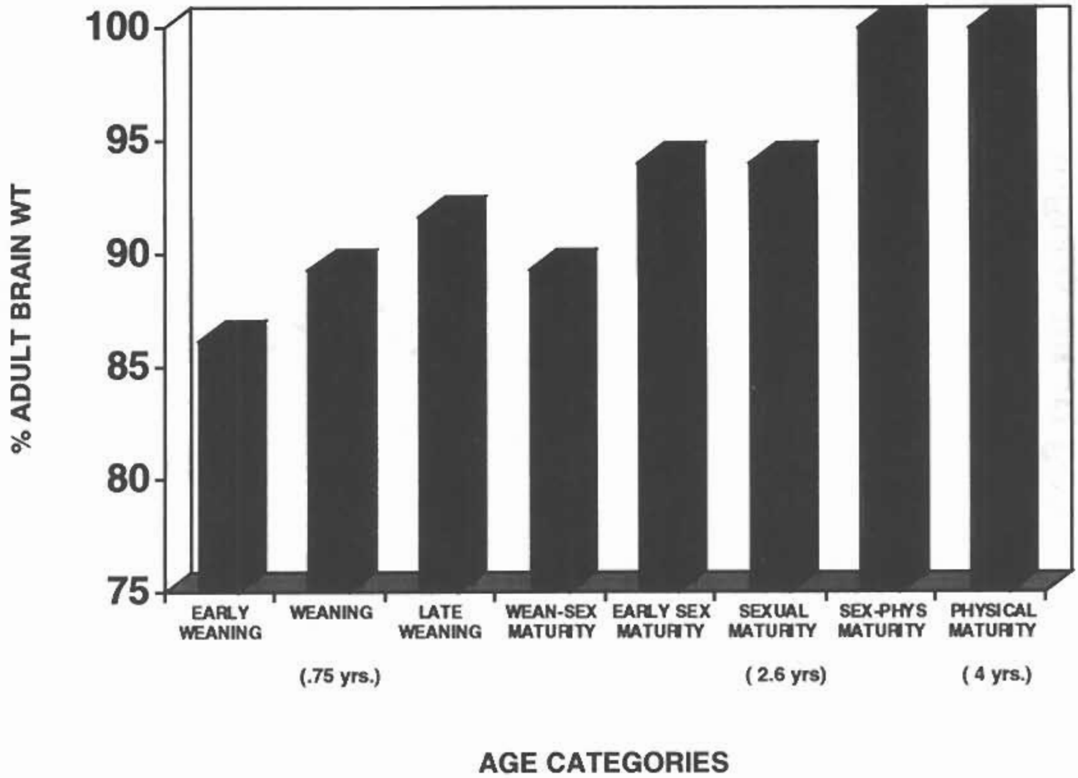

Figure 2. Brain weight as a percentage of adult brain weight at eight age stages for *P. blainvillei*. Mean age for the major stages are also shown.

Figure 2 depicts mean brain weight as a percentage of mean adult brain weight within each of the eight age categories and the mean age for each major category. Figure 2 shows that by weaning age the brain of *P. blainvillei* is almost 90% adult brain weight and by sexual maturity *P. blainvillei* has obtained 94% of adult brain size. Full adult brain size is obtained some time between the age of sexual maturity and physical maturity.

Discussion

The results of the present regression analysis of brain weight and body length are not inconsistent with the findings of Pirlot & Kamiya (1975) in which a growth rate of 0.66 was found. The difference in slopes, as well as the difference in the Pearson correlation values of 0.75 and 0.48 in Pirlot & Kamiya (1975) and the present study, respectively, are explainable by the fact that the sample in Pirlot and Kamiya's study extended over a larger range of body lengths. Furthermore, Pirlot and Kamiya's study included a number of specimens of a younger age than in the present study, thereby including data from a period during which brain size changes more rapidly than later on.

The overall results of the present study are made more meaningful, however, when placed within the context of comparisons with other cetacean and non-cetacean species. Ridgway & Brownson (1984) found that *Tursiops truncatus*, *Delphinus delphis*, and *Orcinus orca* possess neonatal brain weights of 42.5, 57.0, and 53.0% of adult brain weight, respectively. Although no neonates were part of the present sample, the finding that 86% of adult brain weight is achieved by early weaning in *P. blainvillei* suggests that *P. blainvillei* ranks higher than *D. delphis* in terms of neonatal brain maturity. By weaning time at age 18 months Atlantic coastal *T. truncatus* have brains that are approximately 84% adult weight (Ridgway & Brownson, 1984). In the present study *P. blainvillei* was found to possess close to 90% adult brain weight by full weaning age (which is at approximately 9 months of age). Furthermore, the findings of Pirlot & Kamiya (1975) also show that *P. blainvillei* are born with brains relatively mature in size in comparison with *Stenella coeruleoalba*. Therefore, the present findings, when taken together with previous studies, converge upon the conclusion that *P. blainvillei* is born with a more mature brain (in terms of size) and maintains a higher level of brain maturation throughout development than several other odontocete species.

Despite possessing a higher level of brain maturation (in terms of percentage of adult size) than the odontocete species mentioned above, *P. blainvillei* does not achieve as high a level of encephalization as these other species. At adulthood, *P. blainvillei* possesses an EQ (based on the index by Jerison, 1973) of 1.67 whereas *T. truncatus*, *O. orca*, *D. delphinus*, and another *Stenella* species, *S. longirostris*, possess EQ values within a range of 2.57 to 4.26, indicating that *P. blainvillei* is highly encephalized compared with other mammals but not nearly as much as *T. truncatus*, *O. orca*, *D. delphinus*, and *Stenella*.

In general, the present findings are consistent with the basic mammalian pattern by which organisms with higher adult encephalization levels are born at a more altricial level and require more time to achieve adult stages than those with lower encephalization levels. The above findings specifically parallel the pattern within the Primate Order. For instance, modern humans, with the highest encephalization level (EQ=7) of all mammals are born with a brain only about 25% adult size, whereas *P. troglodytes* (common chimpanzee), with an adult EQ 2.34, is born with a brain approximately 33% of adult size (Marino, 1995).

The present study provides corroboration of previous findings as well as new data presented within a comparative context. Although many other factors (e.g. body size, metabolism, ecology) contribute to patterns of brain development across species, the present study exemplifies one way in which comparisons of cetacean biological and life history patterns with those of other mammals can elucidate issues about whether cetaceans can be understood within the larger mammalian framework. A fuller understanding of life history patterns in cetaceans is important both from the standpoint of basic knowledge, theories about general mammalian evolution, and ever-increasing conservation concerns about cetaceans.

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